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Relationships between the hydrological structure, chlorophyll and zooplankton biomasses in the Gulf of Guinea

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Abstract. In the deep-sea part of the Gulf of Guinea, zooplankton dry weights (D.W.) are negatively correlated with the top of the nitrate gradient (D_{NO3}) or the shallowest undersaturated oxygen level (D_{ox}). This is the consequence of a two-fold relation: the integrated chlorophyll, Chl a_i, vs. D_{NO3} or D_{ox} relation in typical tropical structures (i.e. with no nitrate in the mixed layer) and the linear relation between D.W. and Chl a_i for offshore oligotrophic areas and the equatorial divergence as well. However this D.W.-Chl a_i relation is not valid any more in the Mauritanian coastal upwelling. This point is discussed together with that of the respective vertical distributions of zooplankton and chlorophyll and the limits of the studied relations.

Introduction

One of the marine planktologist's aims is to establish simple relations between standing crops of living organisms and parameters of the environment, for a predictive purpose and because his data are often scarce. When studying the two-layered tropical ocean, the planktologist may use the hydrological structure instead of discrete parameters, such as the sea-surface temperature or chlorophyll. Thus, Herbland and Voituriez (1977 and 1979) and Eppley *et al.* (1978) showed recently that the integrated chlorophyll 'a' (Chl a_i) and primary production values were negatively correlated with the thickness of the mixed layer or the depth of the thermocline. The latter may be defined as the depth of either the maximum thermal gradient (D_{GTmax}) or the top of the nitrate gradient (top of nitracline, D_{NO3}) or the top of the oxycline (D_{ox}), all three depths being correlated with one another and with the depths of the maxima of chlorophyll ($D_{Chl\,amax}$) and, within limits, of ^{14}C production ($D_{Prodmax}$). The two-layered structure is a permanent feature of the tropical ocean except for some seasonal upwellings in limited areas. In such a system, 'where the {upper} mixed layer is nitrate depleted, the top of the nitracline has important biological signification. At this level, the light and nutrients combination is optimal {for phytoplankton}. Then, the chlorophyll and the primary production maxima stand at this level, which also corresponds to the maximum uptake of nitrate. The upper layer is oxygen saturated and the lower is undersaturated' (Herbland and Voituriez 1979).

If integrated chlorophyll values are negatively correlated with the depths of the thermocline, oxycline or nitracline, the zooplankton standing crops may be also because of the trophic link between phytoplankton and zooplankton. To relate zooplankton to hydrological observations, the standing crops of phytoplankton and zooplankton should be simply related. Therefore, much attention will be paid to this particular point which has been the subject of numerous studies (e.g. Menzel and Ryther 1961, Blackburn 1966, 1973, Taniguchi 1973, Cushing 1975, Dandon-

neau 1975, etc...).

This paper uses Herbland and Voituriez (1977 and 1979)'s data on Chl a_i and hydrology and subsequent data that have been collected since 1976 during R/V Capricorne cruises in the Gulf of Guinea.

Methods

(a) Station positions (Figure 1)

The area studied extends from 15°N to 15°S and from 10°E to 25°W. Data were collected in *the open ocean only* during the following cruises (the first two numerals of the cruise number refer to the year): CAP 7314 (Stretta 1975), a transect between 1°N and 12°S on 10°W; CAP 7502 (Herbland and Voituriez 1977) consisted of two transects, one from Angola to St Helena Island, the other from St Helena to Abidjan (Ivory Coast); CAP 7506 (Herbland and Voituriez 1977), a transect between Abidjan and St Helena; GUIDOME (groupe Mediprod 1977) off Cape Verde Islands in 1976; CAP 7706, a transect between Abidjan and 6°S on 4°W; CAP 7802 (Voituriez 1980) and CAP 7906 were two transects between Abidjan and St Helena during the upwelling period and the warm season (typical tropical structure) respectively. Data were collected during '*short* stations' (about three hours in length) and 2-5 day stations where measurements of the same parameters could be made several times. There are 21 so-called '*long* stations', identified with A to T letters and GUIDOME (for further details, see Le Borgne, in press).

(b) *Hydrological and phytoplankton measurements*

At each station, 12 sampling levels for nitrate and chlorophyll 'a' analysis were chosen from temperature, salinity and oxygen profiles made with an *in situ* Bissett-Berman STDO probe system, coupled with a Hewlett-Packard computer. Sampling depth intervals were closer in the thermocline so that the key-points of the vertical distribution would not be missed. Nitrate was analyzed at sea according to Strickland and Parsons (1972), chlorophyll 'a' according to Herbland and Voituriez (1979), i.e. by extracted fluorescence before and after acidification to avoid interference with phaeophytin. Such chlorophyll measurements have been made since 1975, the previous ones being by *in vivo* fluorescence with spectrophotometer calibration at several depths. Primary production was measured *in situ* with ^{14}C during 8-11 hours according to Herbland and Voituriez (1979).

Chlorophyll 'a' values were integrated with the usual trapezoid method from 150 to 0 m, and included the deep chlorophyll maximum in any case. The top of the nitracline (D_{NO3}), the first oxygen-undersaturated level (D_{ox}) and the depth of the maximum thermal gradient (D_{GTmax}) were chosen automatically for the typical tropical structure (i.e. with no nitrate in the mixed layer) as follows: D_{NO3} is the shallowest level where nitrate concentration is ≥ 0.5 μg.at.l^{-1}, D_{ox} where oxygen saturation percent is $\leq 95\%$ and D_{GTmax} is the depth of the greatest thermal gradient along the water column.
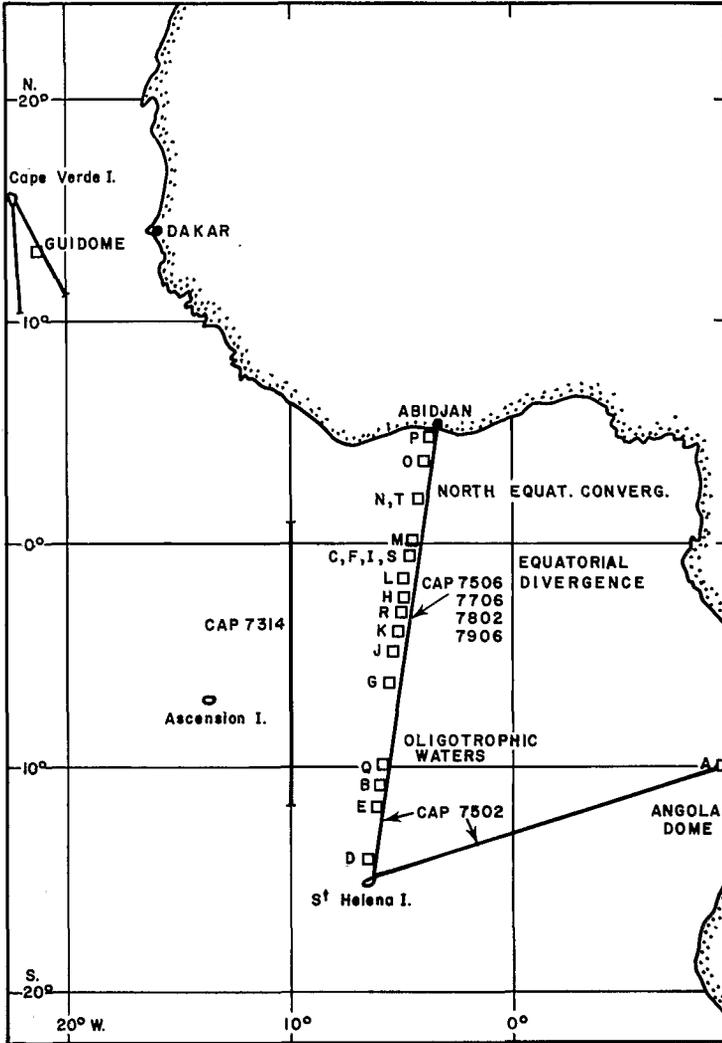
Fig. 1 Short stations transects and long-duration stations positions (square).

(c) Zooplankton biomass measurements

Strictly speaking, the biomass is the living or wet weight of a plankton sample. By extension, we shall use this term for the dry weight (D.W.) or the ash-free dry weight (A.F.D.W.). Both weights were measured according to Le Borgne (1975a): as soon as they were caught, zooplankton samples were rinsed and dried at 60°C for 24 h and deep-frozen until they were weighed. The A.F.D.W. is measured on samples which have been burnt at 550°C for 1.5 hour. The A.F.D.W. value is close to the organic matter and therefore, is a better estimate of the biomass when various planktonic populations are to be considered (Le

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Borgne 1975 b).

Zooplankton is grouped into two size-classes: (1) the *mesozooplankton* which is caught with a WP-2 net (Unesco 1968, 200 μm meshsize), and is sieved on a 5 mm metal screen; (2) the *microzooplankton*, caught at long stations from 100-0 m with a 50 μm net (same length as the WP-2, but with a 49 cm mouth diameter) and is sieved on a 200 μm nylon silk. At the short stations, mesozooplankton was caught by vertical hauls from 0-200 m in 1973-1976 and 0-500 m in 1977-1979. In order to have comparable biomass data, 0-100 m hauls will be used since they were made at all long stations. Because of different hauling depths, long and short stations will be considered separately.

Biomass values are expressed as mg.m^{-2}. In order to take the diel variations into account, they are the means of hauls made every four hours at the long stations. Such a diurnal periodicity may be seen in hauls from 0-200 m but not in those from 0-500 m in the Gulf of Guinea (Le Borgne 1977, In prep.). Lastly, countings of copepods were achieved on WP-2 samples at the long stations and expressed as number of individuals per square-meter.

(d) Zooplankton vertical distribution

At long stations, 2 vertical profiles were made each day at about 8 a.m. and 3 p.m. with a set of eight 30 l Niskin bottles. Sampling depths were chosen from STDO probe and chlorophyll profiles. Water was filtered on a 200 μm silk. Copepods were counted and all plankton animals were transferred onto a Gelman glass-fiber filter for phosphorus analysis according to Menzel and Corwin (1965) (see Le Borgne 1975 a for details). Then, zooplankton concentrations were expressed either in numbers of copepods or in mg Phosphorus per cubic meter.

(e) Statistical analysis

The correlation coefficient, r, and the regression line equation were computed for each relationship between zooplankton and the various parameters.

Because the value of the correlation coefficient may be biased by the distribution of one of the variables (Snedecor and Cochran, 1967), especially when there are few data, Spearman's rank correlation coefficient was also calculated. As the two values were always very close, only the simple coefficient appears on tables and figures. According to Dagnelie (1969) and Ricker (1973)'s table 8, when two variables are considered independent, the best functional regression is Teissier (1948)'s or 'GM regression', as named by Ricker:

$$y = \pm x \, (sy \, / \, sx) + \overline{y} \; - (\pm \, sy \, / \, sx) \, \overline{x}$$

(sy, sx and $\overline{x}$, $\overline{y}$, respectively standard deviations and arithmetic means). The slope, sy/sx, can be compared to unity by the 't' test, following Dagnelie (1970, p. 306). However, the calculation of confidence limits of a value y(x) of the GM regression line has no satisfactory solution from a theoretical point of view (Dagnelie 1970) although Ricker recommends using the ordinary confidence limits, as calculated for the usual regression: 'They are a reasonable approximation of the true limits and will rarely lead to incorrect conclusions'. The calculation of the confidence limits of y(x) is given by Dagnelie (1970) or Ricker (1973).

Results

(a) *Relationships at the long stations*

The mesozooplankton biomass-hydrological structure relations. In spite of high correlation coefficients between D_{NO3}, D_{ox} and D_{GTmax} (Herbland and Voituriez 1979), all three parameters have been associated with the mesozooplankton biomass in order to find the better fit. Since the coefficients with A.F.D.W. are not greater than those with D.W., only correlations with D.W. are shown on Figures 2, 3 and 4. The lack of difference between A.F.D.W. and D.W. may be due to a rather uniform faunistic composition of zooplankton in the deep-sea area of the Gulf of Guinea (Le Borgne, In Prep.).

Figures 2 and 3 show the D.W.-D_{NO3} and D.W.-D_{ox} relations for the 10-11 long stations of the typical tropical structure with no nitrate in the mixed layer. Station D values (in the Benguela drift) were not used in the correlations following Herbland and Voituriez (1977), because its mixed layer is not nitrate depleted while its thermal gradient is deep and sharp, both characteristics being typical of
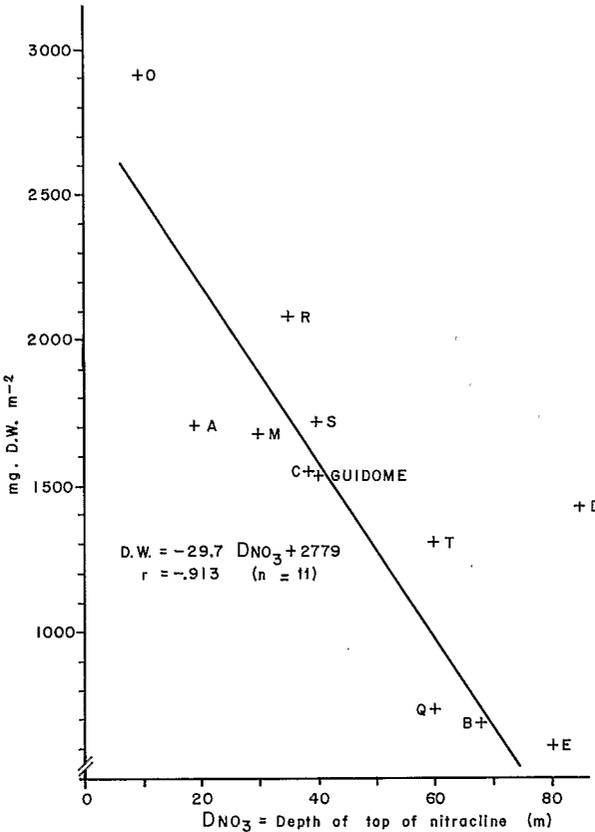

Fig. 2 GM linear regression between mesozooplankton dry weights (D.W.) and the depth of the top of the nitracline (D_{NO3}) for long stations of the typical tropical structure (letters refer to station numbers).

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upwellings and tropical structures. As a result, Chl a_i is greater than expected from the general relation, and the same occurs for D.W.

In Figure 4, there appears to be two relationships, one for A, B, C and Q stations and another for O, R, S, T, E and M stations. This pattern is observed with Chl a_i also, as illustrated on Figure 4: D.W.-D_{GTmax} and Chl a_i-D_{GTmax} points are very close in most cases. The two relations, instead of the single one, may look surprising since Herbland and Voituriez found a good correlation between Chl a_i and D_{NO3} ($r = .80$, $n = 56$) and D_{NO3} and D_{GTmax} ($r = .90$, $n = 123$) on data prior to 1976.

The mesozooplankton dry weight-integrated chlorophyll relations. Figure 5 shows the 17 points of the relationship between D.W. and Chl a_i for the typical tropical structure and for upwelling stations as well. There is no significant improvement of r when the sum of mesozoo- and microzooplankton D.W. are considered: $r = .799$ *vs* $.859$.

In order to display a greater range of Chl a_i values, results from the CAP 7307 cruise in the Cape Timiris upwelling (Le Borgne 1978) were plotted together with those of the Gulf of Guinea (Figure 6). From a strict point of view, the two kinds of data are not exactly comparable: in the Mauritanian upwelling, depths were
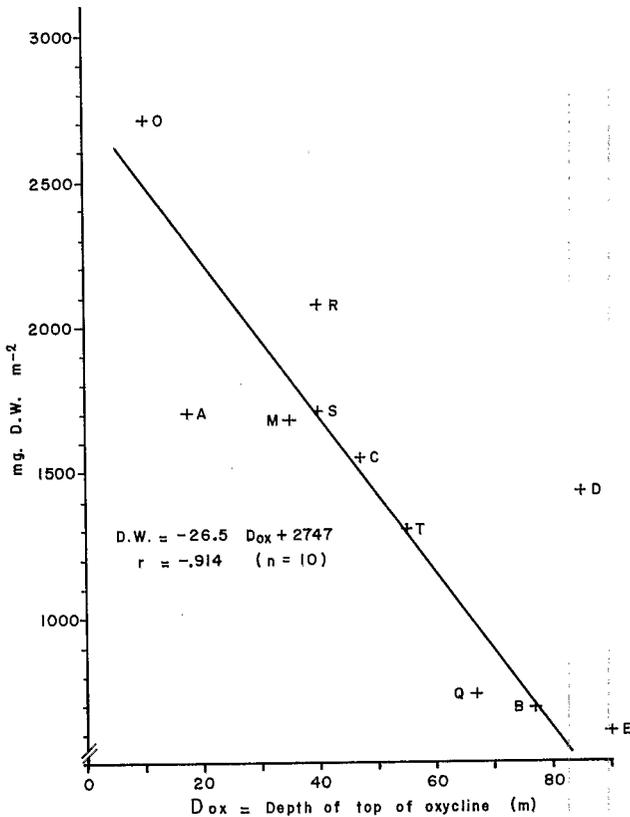

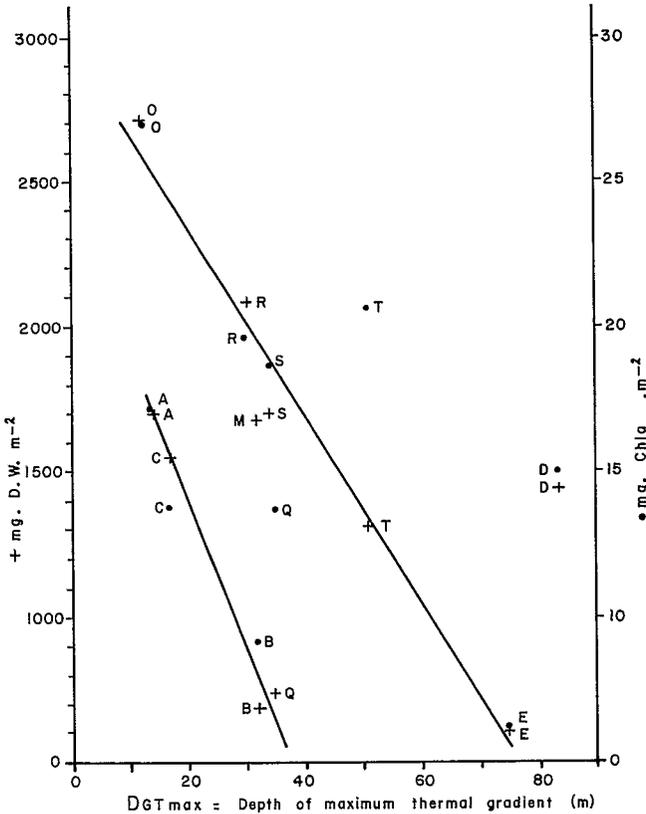Fig. 3 Same legend as Fig. 2, but for the depth of the top of the oxycline, D_{ox}.

Fig. 4 Same legend as Fig. 2, but for the depth of the maximum thermal gradient, D_{GTmax}.

only 20-50 m and Chl a was measured by *in vivo* fluorescence according to Herbland and Voituriez (1974). Still, Figure 6 shows two stations of the Mauritanian upwelling belong to Figure 5 equation; both were situated at the point of upwelling, where surface nitrate concentrations were about 20 μg.at.l^{-1} and chlorophyll rather low. The other points of Figure 6 do not follow the equation found in the Gulf of Guinea and display a very variable D.W./Chl a$_i$ ratio. They belong to stations that are located south of the point of upwelling, where phytoplankton was growing and nitrate was being taken up. Then, the linear relation found in the deep-sea part of the Gulf of Guinea, is not valid in high chlorophyll concentrations of the coastal upwelling of Mauritania.

Relationships between the depth of mesozooplankton biomass maximum (D_{ZKPmax}) and those of chlorophyll ($D_{Chl\ amax}$) and ^{14}C primary production ($D_{Prodmax}$), D_{NO_3}, D_{ox} and D_{GTmax}. Relations between integrated chlorophyll and zooplankton biomasses may be explained as the result of trophic relationships, one aspect of which is the respective vertical distributions of zoo- and phytoplankton. A particular point to be examined, is the location of the depth of the zooplankton maximum with respect to the depth of the maximum of
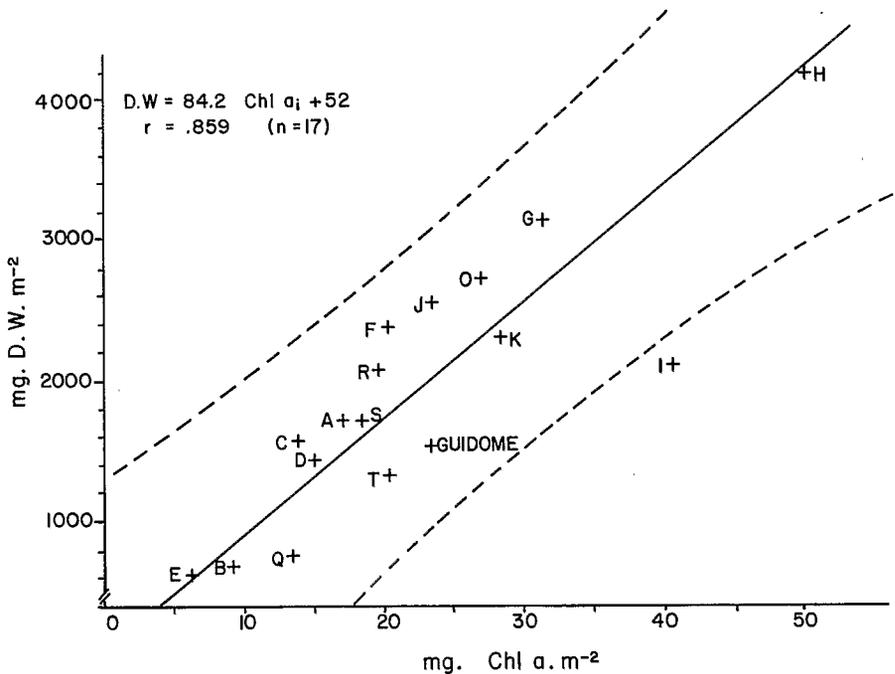
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Fig. 5 Same legend as Fig. 2, but for integrated chlorophyll (Chl a_i) and for both typical tropical structures and upwellings. Dashed curves: 95% confidence interval.

phytoplankton and of the hydrological structure parameters. GM regressions and correlation coefficients of the relations between D_{ZPKmax} and $D_{Chl\,amax}$, $D_{Prodmax}$, D_{NO3}, D_{ox} and D_{GTmax} are shown on Table I. It should be noted that the D_{ZPKmax} is the phosphorus one because it is a deep maximum, as opposed to the maximum of copepod numbers which can occur at the surface at several stations. This difference between the depths of phosphorus and number of copepod maxima has already been discussed by Le Borgne (1977): the surface maximum is made of small individuals, of low biomass, whereas the deep maximum is made of larger individuals.

All correlation coefficients are significant at the 1% level and the best ones are those with D_{ox} and D_{NO3}, once again. The slopes of the lines of D_{ZPKmax} vs D_{NO3}, D_{ox} and D_{GTmax} are significantly less than unity (p > 0.05), which indicates that the zooplankton maximum is shallower than D_{NO3}, D_{ox} and D_{GTmax}. The slopes of the regressions between D_{ZPKmax} and $D_{Chl\,amax}$ and $D_{Prodmax}$ are not significantly different from unity and therefore, the three levels are the same: the correlation between D.W. and Chl a_i is the result of the animals aggregating vertically on the algae. This point is well documented (see Ortner *et al.* 1980 for review and works of Voituriez and Dandonneau 1974, Herbland and Pagès 1975, Le Borgne 1977) although a different pattern was observed by Longhurst (1976) in the oligotrophic tropical Pacific ocean: the zooplankton maximum is associated with the primary production maximum and the chlorophyll one is
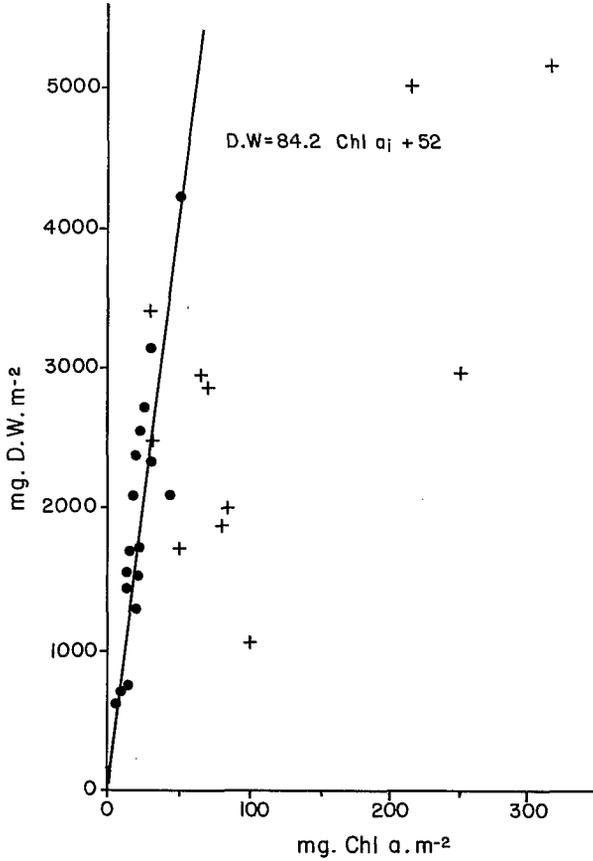
$$D.W = 84.2 \; Chl \; a_i + 52$$

Fig. 6 Relation between mesozooplankton dry weight and integrated chlorophyll at long stations in the Gulf of Guinea (dots) and during the drogue experiment in Cape Timiris (Mauritania) coastal upwelling (crosses).

below. According to Longhurst, grazing would mostly occur at the depth of maximum primary production. Yet, our results do not show a significant difference between $D_{Chl \; amax}$ and $D_{Prodmax}$, thus confirming Herbland and Voituriez (1979)'s observations.

(b) *Relations at short stations*

A similar study will be achieved for the short stations that may be separated into two groups: CAP 7314 and CAP 7506 transects with 0-200 m hauls and CAP 7706, CAP 7802 and CAP 7906 transects with 0-500 m hauls. Biomasses of the latter are significantly greater than the biomasses of 0-200 m hauls and, moreover do not display diel variations (Le Borgne 1977 and In Prep). Only the D.W. will be dealt with since A.F.D.W. lead to identical correlation coefficients.

In Table II a striking point is that correlation coefficients between D.W. and D_{NO3} or D_{GTmax} are significant for 0-200 m hauls but not for 0-500 m ones, in

Table I. GM regressions and correlation coefficients, r, between the depth (m) of zooplankton maximum, D_{ZPKmax} (as phosphorus) and the depths of the tops of nitracline (D_{NO3}) and oxycline (D_{ox}), of the maximum thermal gradient (D_{GTmax}) and of maxima of chlorophyll "a" ($D_{Chl\ amax}$) and ^{14}C production ($D_{Prodmax}$). n = number of stations; *, **, *** are 5, 1 and 0.1% levels of significance for r.

GM regression line	n	r
$D_{ZPKmax} = 5. + .79\ D_{NO3}$	49	.747***
$D_{ZPKmax} = 2. + .83\ D_{ox}$	55	.772***
$D_{ZPKmax} = 13. + .66\ D_{GTmax}$	56	.653***
$D_{ZPKmax} = .6 + .94\ D_{chl\ amax}$	55	.697***
$D_{ZPKmax} = 6. + 1.17\ D_{Prodmax}$	29	.552**

Table II. GM regressions and correlation coefficients between zooplankton dry weight, D.W. (mg.m^{-2}), and D_{NO3}, D_{ox}, D_{GTmax} (m) and integrated chlorophyll, Chl a_i (mg.m^{-2}), for short stations. Hauls from 200 to 0 m were made during cruise CAP 7506 in 1975; those from 500 to 0 m, later.

Relationship	Haul depth	n	r	GM regression line
D.W. - D_{NO3}	0-200	32	-.750***	D.W. = 2913 - 26.1 D_{NO3}
	0-500	32	-.346	D.W. = 5077 - 53.0 D_{NO3}
D.W. - D_{ox}	0-200	32	-.645***	D.W. = 3078 - 27.8 D_{ox}
	0-500	25	-.663***	D.W. = 5490 - 56.9 D_{ox}
D.W. - D_{GTmax}	0-200	32	-.620***	D.W. = 2893 - 23.2 D_{GTmax}
	0-500	32	-.207	D.W. = 4574 - 44.3 D_{GTmax}
D.W. - Chl a_i	0-200	28	.600***	D.W. = -276 + 109.2 Chl a_i
	0-500	54	.408***	D.W. = 647 + 77.1 Chl a_i
Chl a_i - D_{NO3}	0-200	17	-.700**	Chl a_i = 37.2 - .335 D_{NO3}
	0-500	31	.250	Chl a_i = -2.6 + .622 D_{NO3}
Chl a_i - D_{ox}	0-200	17	-.671***	Chl a_i = 36.4 - .301 D_{ox}
	0-500	24	-.248	Chl a_i = 51.2 - .452 D_{ox}
Chl a_i - D_{GTmax}	0-200	17	-.703**	Chl a_i = 34.6 - .271 D'_{GTmax}
	0-500	31	.148	Chl a_i = -1.8 + 1.794 D_{GTmax}

spite of a significant coefficient between D.W. and Chl a_i (Spearman's coefficients are the same). The reason is evident on Table II: correlations between Chl a_i and D_{NO3}, D_{ox} or D_{GTmax} are not significant for 0-500 m hauls stations. Then, the explanation has nothing to do with the depth of the hauls, although better D.W.-Chl a_i correlations are observed with the 0-200 m ones, perhaps because they have a greater proportion of chlorophyll-dependent animals than the deeper ones. The explanation is given in the kind of stations in cruise CAP 7906 (CAP 7706 and CAP 7802 were mainly upwelling stations), which took place in April, during a transition season.

Discussion

(a) *The origin of D.W. - D_{NO3}, D_{ox} or D_{GTmax} relations.*

As mentioned before, these are the result of a twofold relationship: the D.W.-

Chl a_i relation and that between Chl a_i and the hydrological structure, in the typical tropical structure.

Chl a_i - D_{NO3}, D_{ox} or D_{GTmax} relations. The reason of such relations was given by Herbland and Voituriez (1979): the value of the chlorophyll maximum along the water column decreases when this maximum gets deeper, for lack of light; since a great part of total chlorophyll is situated at this maximum, there is a direct relation between Chl a_i and the value of the chlorophyll maximum and an indirect relation with its depth; as the latter is about the same as D_{NO3}, D_{ox} or D_{GTmax}, Chl a_i is negatively correlated with all three.

The D.W.-Chl a_i relation. This was taken as a linear relation for the offshore stations of the Gulf of Guinea, between 6 and, at least, 50 mg Chl $a_i.m^{-2}$, i.e. for all long stations and 83% of the short ones. But most studies that were concerned with the ratio of the two standing crops, were generally based on numbers of individuals or plankton volumes and used log-log transformation in order to bring distributions of the variables closer to the normal one, since areas of various richness were considered (Blackburn 1966 and 1973, Dandonneau 1975 for chlorophyll, Taniguchi 1973 for ^{14}C production). Part of their discussion deals with the slope of the log-log line. Blackburn finds it to be less than unity, which means that the ratio between zooplankton standing crop (as numbers of copepods or displacement volumes) and chlorophyll is greater in oligotrophic zones than in the richer ones. However Taniguchi and Dandonneau find slopes greater than 1 when there is equilibrium between phyto- and zooplankton and draw a different conclusion, based as is Blackburn's, on the variations of the ecological efficiency.

Because of this controversy, the log-log transformation was applied to data on short and long stations, although the distribution of neither variables required any transformation. The new correlation coefficient is not significantly different from that in Figure 5 (.885 *vs.* .859) and the new relation is D.W. = 74.5 Chl $a_i^{1.05}$; the slope is not significantly different from 1 at the 5% level of significance. As far as CAP 7506 short stations are concerned, the correlation coefficient on log-log transformed data is .520 (n = 28), instead of .600 in Table II and the relation is D.W. = 32.0 Chl $a_i^{1.36}$, the slope being not significantly different from 1.

Because the slope of the log-log line is not significantly different from unity in either of the two cases, the ratio between D.W. and Chl a_i may be taken as constant in the deep-sea area of the Gulf of Guinea, for typical tropical structures and the equatorial divergence as well. This conclusion, apparently, conflicts with Blackburn (1966 and 1973), Dandonneau (1975) and Taniguchi (1973)'s but may be due to the use of different units for zooplankton standing crops. Thus, Blackburn (1966) like Dandonneau correlate numbers of copepods, instead of D.W. in the present study, with Chl a_i and finds slopes different from unity, just like we do in the Gulf of Guinea (Figure 7): the best fit is a semi-log relation, thus meaning the number of copepod/Chl a_i ratio would be less in rich areas than in oligotrophic areas. The variable zoo-/phytoplankton ratio is observed also with the displacement volume (Blackburn 1973) or the wet weight (Taniguchi 1973), simply because D.W./volume or D.W./wet weight ratios are functions of the size
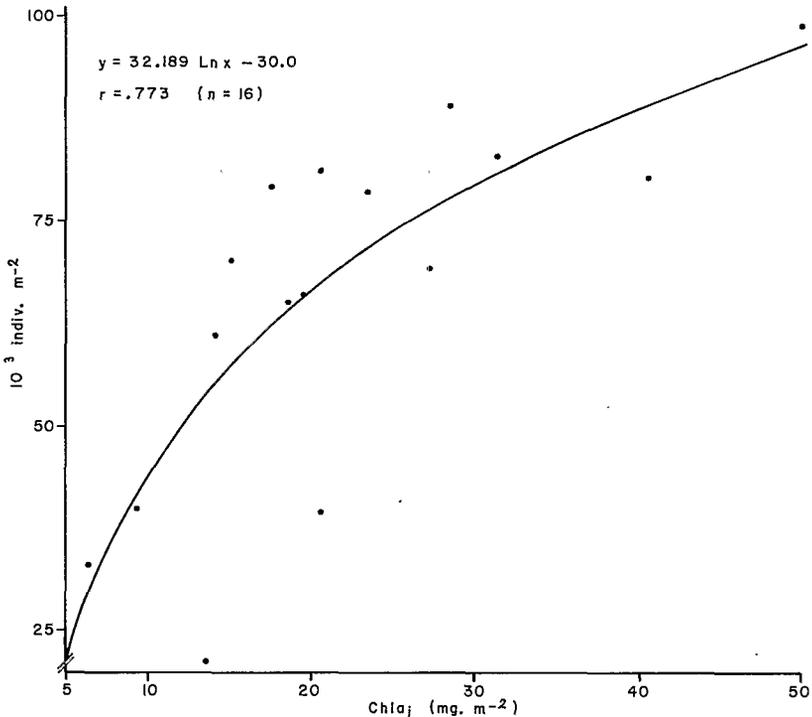
Fig. 7 GM regression curve between the number of copepods and Chl a$_i$ at long stations.

of plankton samples and, thereby, of the richness of the area (Wiebe *et al.* 1975, Le Borgne 1975 b). Then, D.W. should be preferred to the wet weight or volume since it is in better agreement with carbon and gives a better estimate of zooplankton standing crop.

However, when data from the Mauritanian upwelling are examined (Figure 6), the D.W./Chl a$_i$ ratio is less than that in the Gulf of Guinea and much more variable. Such a difference between offshore stations (divergence and gyres) and those of the coastal upwellings has already been pointed out by Walsh (1976) for the phytoplankton-herbivore interface: in contrast to offshore stations, coastal upwellings are subject to an additional variability of the habitat, the time-scale of days to weeks, which corresponds to interactions of phytoplankton and zooplankton life cycles. As a result, phytoplankton and herbivores cycles are not synchronized in space, just as they are not in time in temperate regions. Then, it is obvious that the herbivore:phytoplankton ratio is variable and may even decrease from the point of upwelling to the chlorophyll bloom, as shown by Dandonneau (1975) for the Mauritanian upwelling. Plant standing stocks may not be thoroughly grazed on by herbivores and their decay gives birth to high dissolved organic nitrogen and ammonia concentrations (Le Borgne 1978 for Cape Timiris upwelling). In contrast, Walsh (1976) shows 'the dominant variability of the open-ocean system is associated with a time-scale of months, i.e. 50-100 days, and is thus larger than that of individual phytoplankton-zooplankton interac-

tions'. As a result, the herbivore biomass has enough time to be adapted to phytoplankton variations that are consecutive to variations in the nutrient input, the latter being at least an order of magnitude less than in coastal upwellings in any case (cf. Walsh's table 1). Then, biomass cycles of the two trophic levels are well synchronized and the ratio of zooplankton to phytoplankton standing crops is more or less constant in offshore areas.

Beside its greater variability in the Mauritanian upwelling, the D.W./Chl a_i ratio is systematically less than in the offshore stations of the Gulf of Guinea (Figure 6). This observation would confirm Blackburn (1966)'s opinion on the diminution of this ratio in eutrophic areas, although two other reasons may be put forward instead of his hypothesis of the diminution of the ecological efficiency in rich areas: (1) the first reason concerns the importance of phytoplankton (and chlorophyll) in the zooplankton ration, composed mostly of particle-feeders (Le Borgne 1977 and In Prep.). In coastal upwellings, phytoplankton makes up the bulk of the particles (Hobson *et al.* 1973) and therefore, the bulk of the zooplankton ration; but, in areas poorer in particles, phytoplankton importance decreases (Finenko and Zaika 1970 and Hobson *et al.* 1973) for it is replaced by tripton and heterotrophic organisms and this is so in zooplankton ration. Then, a given zooplankton standing crop needs more chlorophyll in upwelling areas than in oligotrophic ones, provided the gross growth efficiency is the same in either of the two cases (zooplankton net growth efficiency, K_2, was not found to be a function of Chl a_i at the long stations of the Gulf of Guinea by Le Borgne, in press). (2) the second reason for the lower D.W./Chl a_i ratio in the Mauritanian coastal upwelling is that the part played by zooplankton in the total herbivorous standing crop may be smaller than in offshore stations. In other words, for a given chlorophyll value, there could be more zooplankton offshore than in coastal upwellings. Unfortunately, the ratio between zooplankton and total herbivores is not well documented in offshore stations, but it should be noted that no high catches of Clupeidae or Engraulidae (herbivorous fish) that are recorded for coastal upwellings, are found offshore.

In conclusion, zooplankton/phytoplankton ratios may be less in coastal upwellings independently of variations of the ecological efficiency. Alternative explanations are differences in the part played by zooplankton in the herbivores biomass and by phytoplankton in the filter-feeders ration.

(b) *Practical value and limits of the relations*

For the typical structure only, the knowledge of D_{ox} or D_{NO3} makes it possible to assess the zooplankton biomasses. The best relation is the D.W.-D_{ox} one, probably because the STDO continuous oxygen vertical profiles are more precise than the discrete nitrate profiles. Relations are loose when D_{GTmax} is used since the Chl a_i-D_{GTmax} relation is valid only when the vertical advection can be considered as negligible (Herbland and Voituriez, 1979), which only happens in oligotrophic areas. At last, the best relations are those of the 2-5 day long stations, where measurements of the parameters were done several times. At the short stations, both zooplankton biomasses (Le Borgne 1977) and chlorophyll (Le Bouteiller and Herbland, In Prep.) may be more affected by diel variations and

the usual spatial heterogeneity.

When there is no nitracline nor oxycline, i.e. in upwelling situations, the above relations are not valid any more and other hydrological variables should be used. A possible parameter is the value of the vertical thermal gradient which may be expected to be low in new upwelled waters and high in more equilibrated systems. But no significant relation was found between it and D.W. or Chl a_i.

If relations between D.W. and D_{ox}, D_{NO3} or D_{GTmax} are significant in most of the long stations and for CAP 7506 transect, there are exceptions due to the lack of correlation between Chl a_i and the hydrological structure *viz.* station D and CAP 7906 transect. The latter looks like a temporary situation: thus the short stations of the transect do not follow the CAP 7506 Chl a_i-D_{NO3} relation (Figure 8) whereas the long stations (Q, R, S, T) do. These were made from 4 (station Q) to 20 days (station T) after the transect. The influence of diel variations on Chl a_i (as observed by Le Bouteiller and Herbland, In Prep.), or spatial heterogeneity may be left aside since almost all short station values are much greater than expected from CAP 7506 relation (Table II) and do not follow any relation at all. Still the depth of the chlorophyll maximum and D_{NO3} are fairly well correlated ($r = .804$, $n = 30$), which means that part of the chlorophyll follows the hydrological structure. Then, the high chlorophyll values (and the high D.W. ones, too) are the result of either a former hydrological structure or an horizontal
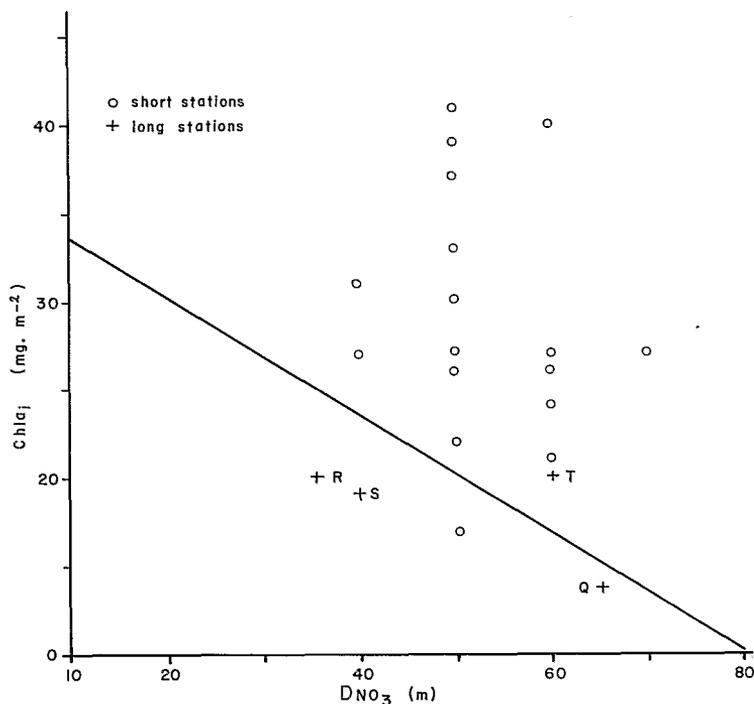

Fig. 8 Relation between Chl a_i and D_{NO3} during 7906 cruise. The line is that of the 0-200 m hauls (CAP 7506 transect) of Table II.

transport. Because the area stretches on as much as 16° in latitude, the latter hypothesis is probably wrong. On the other hand, the studied period was April during which trade winds were moving northwards and made the whole hydrological situation change. Then, the question is to know how often are such relations not valid anymore in the Gulf of Guinea. Except CAP 7906 (April) and CAP 7314 (October), all cruises of the present paper or Herbland and Voituriez (1979)'s took place during well settled hydrological situations, i.e. the cold (July-September) or the warm season (January-March). Therefore measurements should be made in other periods in order to give closer confidence limits to the relations, the anomalies frequency and their explanation. The interest of such relations is evident when the knowledge of phytoplankton or zooplankton standing stocks is required. Besides oxygen or nitrate profiles, other parameters can be used, e.g. the light profiles, as long as they are correlated with Chl a_i and, thence, with zooplankton dry weights in the offshore area.

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